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THE SPECIES AS CATEGORY, TAXON AND POPULATION

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THE SPECIES CONCEPT

It is often said that there is no other problem in biology that is as refractory to solution as is the species problem. And the solutions that have been proposed, from Aristotle, the scholastics, and Linnaeus, to the present time, are highly diverse and often incompatible with each other. This has been convincingly demonstrated by the splendid presentations of the last four days. To an outsider, the picture that emerged from our discussions may seem utterly bewildering. It almost seems as if every author in the history of biology who had ever written on the species problem had his own personal concept, and that we were as far from consensus as ever.

Fortunately, the situation is not quite so discouraging. It is the object of my own presentation to show that there is actually a very limited number of different species concepts, and that the species problem can be brought rather close to solution by a careful philosophical analysis of the terms and concepts used in this field and by an analysis of the process of speciation.

In order to refute erroneous opinions of some philosophers it must be emphasized that the species is not an invention of taxonomists or philosophers, but that it has reality in nature. The existence of species is known to the most primitive human tribes, who recognize species that exist among the animals and plants of their environment and designate them by name. It was a startling revelation to me when I realized more than fifty years ago that the stone age natives in the mountains of New Guinea recognized as species exactly the same entities of nature as the scientists of the western world.

SPECIES CONCEPTS

When one is dealing with evolving biological populations, and that is what species of organisms are, one can not expect the simplicity and unambiguousness which one encounters among parameters in the physical sciences. Also,

the manifestations of species status may differ quite strikingly in different groups of organisms. Yet, I am prepared to suggest that nearly all the species concepts and species definitions that have ever been advanced, and in particular those that were discussed at this colloquium, can be grouped under four headings.

(1) The typological species concept

The word species in its simplest conception simply means "kind", such as when a mineralogist speaks of species of crystals and a physicist of nuclear species. A typological species is an entity that differs from other species by diagnostic characteristics. This was the species concept of Linnaeus and Lyell and was supported by those philosophers from Plato to modern times who consider species to be "natural kinds" or "classes". Members of such a class are characterized by sharing the same species essence.

Philosophical objections to this concept will be discussed below, but it turned out that this species concept lacks even practical utility because it forces its adherents to consider as species different phena within a population, and to lump groups of sibling species into a single species (Mayr 1969). As recently as 1944 the geneticist Sturtevant insisted on combining *Drosophila pseudoobscura* and *D. persimilis* into a single species because this would permit "identifying wild specimens without breeding from them or examining their chromosomes" (1944 : 476).

The discovery of the high frequency of morphologically indistinguishable species (sibling species) has demonstrated the invalidity of the morphological species better than anything else.

Numerical pheneticists adopted the designation *Operational Taxonomic Unit* (OTU) for taxa at various hierarchical levels. One of the putative advantages of this designation at the species level was that it by-passed the need of assembling phena into biological species. In actual practice however it leads to absurdities to treat phena as OTUs, and the OTUs that are recognized in the phenetic analysis are the result of careful, but by necessity subjective, analysis, because otherwise morphs in polymorphic species, age stages, sex differences, and other individual variants, would have to be treated as different OTUs.

Rejection of the morphological species concept, however, does not invalidate the usefulness of morphological criteria for the drawing of inferences on species status. Furthermore, as a first approach in a preliminary analysis of the diversity of a fauna and flora, it is sometimes necessary to recognize tentative species based exclusively on morphological criteria. As will be shown below, such tentative arrangements will be confirmed or rejected or at least modified as soon as additional information becomes available. "It must be emphasized that there is a complete difference between basing one's species concept on

morphology and using morphological evidence as inference for the application of a biological species concept" (Mayr 1969 : 25).

The typological species concept has retained its usefulness in the classification of inanimate objects. Such species are classes of objects characterized by the same defining criteria.

(2) The nominalist species concept

Only individual objects exist in nature according to this concept. Such objects or organisms are bracketed together by a name, and it is by the subjective action of the classifier that it is decided which objects are combined into one species. Species, therefore, are merely arbitrary mental constructs. Species have no reality in nature according to the nominalist. This has been the claim of the nominalists since the Middle Ages and of numerous authors in the 18th century, but also of such recent authors as Gilmour (1940), Burma (1949), and Ehrlich and Holm (1963). Some recent philosophers also have intimated that species are only conventions but have no reality in nature. "The concept of species was introduced to answer to certain theoretical desiderata" (Kitcher, 1984). This claim is refuted by the fact that the concept was developed by the best of the naturalists, beginning with the herbalists of the 16th century and continued by John Ray, Linnaeus, and virtually all naturalists up to the present day. I have always thought that there is no more devastating refutation of the nominalistic claims than the above mentioned fact that primitive natives in New Guinea, with a Stone Age culture, recognize as species exactly the same entities of nature as western taxonomists. If species were something purely arbitrary it would be totally improbable for representatives of two drastically different cultures to arrive at the identical species delimitations. Although a few nominalists still survive, it is now almost unanimously agreed that there are real discontinuities in nature delimiting different species. Each of these species has different biological characteristics, and the analysis and comparison of these differences is a prerequisite for all other research in biology, and indeed all branches of biology. Whether he realizes it or not, every biologist works with species.

A SHIFT TO NEW SPECIES CONCEPTS

As the naturalists, beginning with the 17th century, began to make increasingly careful studies of species of organisms, evidence began to accumulate that these species were something different from so-called species of inanimate objects. These naturalists showed quite conclusively that biological species not only had reality in nature, but also that in many, if not most cases, they were sharply distinguishable from each other by a natural discontinuity.

However, the creation dogma, as well as the prevailing essentialistic philosophy, also postulated such discontinuities, and this favored a continued adherence to the typological concept. This was reenforced by the daily practice of classifying specimens, where the most convenient strategy was to consider as a different species " that which was different ", in other words, that which could be distinguished by morphological criteria.

It was not until the Darwinian revolution that attempts were made to introduce into biology a species concept that reflects the unique properties of biological populations. The criterion " degree of difference " was replaced by the new criterion " absence of interbreeding ". Furthermore, species were now seen as evolving populations rather than as being eternally constant.

(3) Biological species concept

This species concept is based on the observation of local naturalists that at a given locality different populations co-exist that do not interbreed with each other. This is articulated in the definition, " Species are groups of interbreeding natural populations that are reproductively isolated from other such groups ".

Certain aspects and implications of this definition will now be discussed. For instance, since hybridization may occur occasionally between individuals of two different good species, without a breakdown of the isolation between these species, it is important to stress that the term reproductive isolation refers to the integrity of populations, even though an occasional individual may go astray.

If one believes in evolution, then one must accept the conclusion that every species is the product of evolution, or more precisely the product of speciation, and that it must have certain qualities that are the consequence of such a history. It permits the making of certain predictions concerning properties to be assigned to a natural entity which one believes to be a species. These properties are that a new species must have acquired reproductive isolation as a result of the process of speciation, it must have also acquired a new, stabilized, well-integrated genotype, and it will, in most cases, have acquired a species-specific niche.

It is this potential for making predictions which gives the biological species its great strenght. It permits at all times the testing of clusters of similar (or not so similar) populations for their species status. It is the biological species which is the material with which population geneticists work as well as ecologists and students of behavior. When one concentrates on the mentioned biological attributes of species, one almost inevitably arrives at the same species delimitation, whether one is a primitive native of the New Guinea mountains or an ethologist or a student of ecosystems. The clear-cut discontinuities found in nature, when populations are studied at a given locality, are a real phenomenon. It is

the existence of these discontinuities which makes the work of the student of behavior and of the ecologist possible, because every biological species has species-specific behavior patterns as well as a species-specific niche utilization.

Nothing is more misleading than the claim that the biological species concept is not practical. Actually, the biological species concept serves as a yardstick with the help of which controversial or simply obscure situations can be clarified. In an analysis of about 80 controversial cases concerning the status of avian species in North America, Mayr and Short (1970) were able to clarify all but a single one by applying the yardstick of the biological species definition. In an analysis of a local North American flora Mayr and Wood (unpublished) were likewise able to show that by far the majority of the controversial issues (and there were literally hundreds of them) could be resolved quite unequivocally by applying the biological species concept. Shapiro (1982) has shown how helpful the biological species was in clarifying confused taxonomic situations among butterflies. But more than that, he stresses correctly the great heuristic value of this concept. "The prime virtue of the biological species concept, and the reason for its survival despite so many withering polemics, has been its ability to generate interesting questions of evolutionary, biogeographic, and systematic interest about real organisms in the real world" (p. 217).

THE PROTECTION OF THE SPECIES-SPECIFIC GENOTYPE

The question is sometimes asked, why are there species? – why do we not find in nature simply a total continuum of similar or more and more widely diverging individuals? (Mayr 1957). It is now clear that the isolating mechanisms of a species are a protective device for well-integrated genotypes. Any interbreeding between different species would lead to a breakdown of well balanced, harmonious genotypes, and would quickly be counteracted by natural selection. Such counterselection against hybridization has been demonstrated in nature in literally thousands of cases, even though cases of successful hybridization, particularly in plants, have also been demonstrated.

The high selective value of mechanisms that help to maintain the integrity of species-specific genotypes is documented by the diversity of isolating mechanisms (Mayr 1963, Chap. 5) and by the fact that the isolation is usually effected not by a single mechanism but by a set of them. In numerous cases, particularly in plants but also in certain groups of insects (morabine grasshoppers), sterility is the principal or sometimes even exclusive isolating mechanism. In most animals, however, behavioral barriers are all-important. Males approach females and test them for their receptivity. There is an interchange of stimuli or signals between male and female, and if the female is receptive and the signals sent out by the males appropriate (that is, conspecific), the courtship will proceed to copulation.

The specific reaction of males and females toward each other is often referred to loosely as "species recognition". "This term is somewhat misleading,

since it implies consciousness, a higher level of brain function than is found in lower animals (see also Spurway 1955) " (Mayr 1963 : 95). In recent years Paterson (1976, 1984) has again revived the recognition definition of the behavioral isolating mechanisms, without referring to the arguments why this definition had been rejected by earlier authors. It must be emphasized that there is no argument about the biological facts but only about the terminology. As I said in 1963 : " Species recognition, then, is simply the exchange of appropriate stimuli between male and female, to insure the mating of conspecific individuals and to prevent hybridization of individuals belonging to different species " (1963 : 95).

In the process of the rejection of nonconspecific mates and the acceptance of conspecific mates, one can focus attention on either one or the other of these two processes. Rejection means maintaining isolation and acceptance means recognition. These are simply two sides of the same coin. When I prefer the term isolation to the term recognition, which I had been fully aware of but rejected in 1963, it is for two reasons : first because recognition, as I said, postulates a degree of conscious cognitive activity that is not to be expected in " lower " animals, and secondly because isolation among species is effected in numerous species or organisms by isolating mechanisms other than behavioral ones. There is, for instance, no mate behavior recognition among morabine grasshoppers and many other organisms with post-zygotic isolating mechanisms.

Where Paterson is right is in pointing out the probable primacy in the acquisition of behavioral isolation as compared to niche acquisition (Mayr 1984 : 6-7).On the other hand, acceptance of the term isolating mechanisms does not necessitate acceptance of either the Darwin-Muller-Mayr or Wallace-Dobzhansky theories of the origin of reproductive isolation. Likewise (contra Vrba 1984) it does not matter whether one accepts the isolation or recognition terminology when it comes to the evaluation of the species status of isolated populations.

EVOLUTIONARY THEORY AND THE BIOLOGICAL SPECIES CONCEPT

Curiously, the fact that species are the product of evolution and that, owing to the genetic turnover in populations, all species are evolving all the time, has been used both as evidence in favor of the biological species concept and as evidence against it. Every deme evolves and so does every subspecies as well as every higher taxon (aggregate of species). Therefore the fact of evolving is not in the slightest diagnostic for the species. Alfred Emerson (ms. and 1946) had " evolving " in his species definition, but in 1942 I rejected this inclusion as obviously not being a defining characteristic of species.

The internal cohesion of the species is continuously reinforced by interbreeding. However such interbreeding is also stressed in the pre-

evolutionary species definition of Cuvier, and (by implication) even in that of John Ray. But such a recombination of the genetic characteristics of populations could simply be a reshuffling of the features of the originally created ancestors. This is evidently the way it was seen by authors like Ray and Cuvier. Being spatio-temporally restricted and internally cohesive they had all the characteristics of "individuals" (Ghiselin 1966, Hull 1975) and yet they were not evolving.

From the beginning various authors have rejected the biological species concept more or less emphatically (Sokal and Crovello 1970, Sokal 1973, Ehrlich 1961, 1980, 1982, and Raven 1977a, 1977b). The objections are virtually never raised against the biological species concept as such, that is the occurrence in nature at a given locality of coexisting, reproductively isolated populations, but rather against the expansion of this nondimensional concept in space and time. Almost invariably there is a confusion between the species as a category (as expressed in the species concept) and the species as a taxon, a more or less well delimitable aggregate of populations. Nowhere are there two aspects of the species (category vs. taxon) more completely confounded than in the discussion by Sokal and Crovello (1970). Those who come from mathematics into biology would like species to be typologically fixed in space and time, and as invariable as possible. When they find that the population structure of species as well as the processes of evolution make such an ideal typological species impossible, they consider this a refutation of the biological species concept. Actually such variation and evolutionary change can be used as an objection to any species concept so far proposed (see also below). Species taxa, as we shall see, are based on inference from the species concept. That there are operational difficulties connected with the making of such inferences does not refute the concept as such, as Hull, Wiley, and others have pointed out. It is rather ironical that some authors (e.g. Raven) who have criticized the biological species concept in theoretical papers, seem to adopt it completely in their own taxonomic monographs and in those of their students. Numerous authors in recent years have refuted the putative objections to the biological species concept (Hull 1970, White 1978, Willmann 1985 : 52-54, De Jong 1982 : 233, Ghiselin 1985), papers in which the various objections to the biological species concept are carefully considered. One objection made particularly often is the curious one that species such as documented in the biological species concept do not exist in nature. This claim is easily refuted by any study of a local fauna or flora (Mayr and Short 1970, Mayr and Wood 1985).

NICHE OCCUPANCY AND SPECIES DEFINITION

Coexisting species are not only reproductively isolated, but occupy niches that are sufficiently different to preclude competitive exclusion (Gause). Numerous distributions of closely related species are known in which these species are separated by a parapatric border. Various kinds of evidence lead in

these cases to the inference that the parapatric species compete for the same niche but that one is superior on one side of the borderline, the other species on the other side. Sympatry can be achieved in such cases only when these species acquire niche differences. I incorporated this conclusion in a recently suggested species definition : " A species is a reproductive community of populations... that occupies a specific niche in nature " (1982 : 273). This reference to the ecological specificity of a species was criticized by Ghiselin (in press) as either superfluous or as confounding " professions with organizations ". There is some justification to this critique, but it fails to come to grips with the important fact that absence of reproductive isolation is not the only factor that prevents the harmonious coexistence of species. Somehow I have the feeling that a neospecies that has not yet acquired the necessary ecological autonomy to co-exist with a sister species has not yet acquired full species status.

Attempts have been made to make ecological differentiation the primary species criterion rather than reproductive isolation (Van Valen 1976). This however, leads to insuperable difficulties. In most species with geographic variation, particularly in polytypic species with numerous isolates, it is found that many of the local populations differ in their niche utilization. One would have to make each of these variant subspecies a different species. Furthermore, there is now good evidence for polymorphism for niche utilization even within a single population. All this makes it impossible to make ecological differentiation the primary species criterion.

(4) The evolutionary species concept

The application of the biological species concept to multidimensional assemblages of populations always encounters difficulties. Paleontologists who study species distributed in the time dimension have been searching for some time for a species concept that would be particularly suitable for the discrimination of fossil species. After Meglitsch (1954) it was particularly Simpson (1961), Wiley (1980, 1981), and Willmann (1985) who have attempted to develop a species concept particularly suitable for paleontology and phylogenetic researches. Simpson's definition (1961 : 153) was :

" an evolutionary species is a lineage (an ancestral-descendent sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies ".

Wiley (1981 : 25) has slightly modified it to read :

" an evolutionary species is a single lineage of ancestor-descendent populations, which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate ".

It would seem that such definitions abandon the clear-cut criteria of the biological species definition (reproductive isolation) and replace it by such undefined vague terms as " maintains its identity " (does this include geo-

graphical barriers?), "evolutionary tendencies", and "historical fate". What population in nature can we ever classify by its "historical fate", when this is entirely in the future? In addition, the evolutionary species concept encounters three major difficulties.

(1) It is applicable only to monotypic species. It is unable to cope with polytypic species that contain geographical isolates, because each of these isolates answers the evolutionary species concept, being a single lineage which maintains its identity. Thus the definition provides no yardstick for the placement of isolated populations. When very similar morphospecies are encountered at different exposures, the evolutionary concept provides no criterion that would permit a decision whether or not they are conspecific. Rather, as in the biological concept, one has to infer from the amount of morphological difference exactly as one does with geographical isolates in the living fauna.

(2) The qualification "own evolutionary tendency and historical fate" does not permit discrimination between good species and isolates. There are no empirical criteria by which either evolutionary tendency or historical fate could be observed in a given fossil sample. Simpson himself (1961 : 154 - 160) realized this, and admitted arbitrariness in application.

(3) The hoped for capacity of an evolutionary concept to help in the delimitation of chronospecies did not materialize. This is well documented by the inability of the evolutionary species concept to arbitrate in the controversy between Gingerich and his followers, who believe in a frequent occurrence of phyletic speciation, and Stanley, Eldredge and followers who believe in a complete stasis of all neospecies. Indeed, the three most articulate proponents of the evolutionary species concept (Simpson, Wiley, Willmann) agree that it does not provide a nonarbitrary method for the delimitation of species in the time dimension. This is most curious, since the main reason why the evolutionary species concept was introduced, was in order to deal with the time dimension, which is not considered in the non-dimensional biological species concept.

Since time is one of the factors involved in the problem of speciation, it is necessary to discuss the problem of the modes of speciation in order to have a basis for developing criteria for the delimitation of chronospecies. A chronospecies is delimited by its birth (origin) and its death (extinction). With respect to the delimitation of species taxa, the following tabulation of modes of origins of new species might be helpful :

POTENTIAL ORIGINS OF NEW SPECIES

A) Through a speciation event

a) Instantaneous (e.g. polyploidy, stabilized hybrid)

b) Very rapid (peripatric speciation, conceivably sympatric speciation)

B) Without a speciation event (parental species transformed)

c) Dichopatric speciation (split by a geographic barrier with gradual divergence).

d) Gradual phyletic transformation of a single lineage.

The question to be answered is : In which of the four potential modes of speciation is it possible to determine the point of origin of a new species? This is clearly possible in the two cases in which the new daughter species originates either instantaneously (A a) or so rapidly (A b) as to be instantaneous as far as paleontology is concerned. However, the parental species remains in both cases (A a and A b) unchanged or at least does not change its species status.

Neither Hennig (1950) nor Willmann (1985) allow for the process of peripatric speciation, that is for the budding-off of a new daughter species, and thus their claim that every speciation event inevitably terminates the life of the parent species is clearly wrong. This is fully understood by Wiley (1981 : 34-35). For instance, when the New Guinea kingfisher *Tanysiptera galatea* produced daughter species on Koffiao, Biak, Numfor, Tagula, and the Aru islands, this did not affect the parent population on the mainland of New Guinea (Mayr 1954). It would have been quite absurd to have ranked the mainland population as a new species every time it sent off a founder population to one of the adjacent islands.

This same species (*Tanysiptera galatea*) also shows the inapplicability of another of Hennig's principles for the delimitation of populations and closely related allopatric species. The daughter populations on the adjacent islands are not derived from the mainland species as a whole, but it is always a single local population of the widespread continental species that produced a given founder population. Surely, one can not divide the mainland species into a number of separate species because five local populations have become the "stem species" of the five island species.

In all cases where several isolated populations of a polytypic species have completed speciation and the polytypic species has become a superspecies with a set of allospecies, it is impossible to arrange these in the form of an unambiguous cladogram, or at least a dichotomous cladogram. It is made impossible by the fact, as explained above, that each of the derived species is most closely related to one localized population of the mainland species, and by two additional considerations. Evolution in the isolates may represent mosaic evolution, and aspects of both reproductive isolation and morphological characters may be acquired unequally in the different isolates. Furthermore, with the derivatives of the parental species all having the same or similar potential, it is likely if not probable that several derived species will acquire the same character independently. This is well illustrated by the allospecies of the *Xiphophorus helleri* superspecies of Central America (Rosen 1979) and the species of *Lapidochromis* of Lake Malawi (Lewis 1982).

In categories B c and B d, the parental species is being transformed. Even in the cases where a species splits into two (B c), the two daughter species are virtually identical at the moment of the split, and if any species difference evolves in the two separated lines, it is by gradual transformation. This makes it impossible to designate a precise point of origin of the new daughter species. This would be equally true if the process of gradual phyletic transformation (B d) occurs, as is supported by many paleontologists. They believe that a temporal sequence of species can indeed be produced by gradual phyletic evolution and that in such a case the line between two sequential species must be arbitrarily placed between one generation of the parental species and its daughter generation, which now belongs to the new species. That a "subdivision of unbroken successions of species... must be arbitrary" was frankly admitted by Simpson (1961). These findings can be summarized by saying that the origin of a new species can be reasonably well pinpointed in the two cases A a and A b, but that it is largely arbitrary where one places the point of origin of the new species originating in categories B c and B d.

The termination of chronospecies encounters equivalent difficulties. There are three potential modes of a termination of species.

a) By traditional extinction, like that of the dodo or the passenger pigeon, without any connection with speciation. What percentage of species terminate in this manner is still controversial. According to the more extreme punctuationists (Stanley, Eldredge/Gould), this is the normal fate of all species. Once they have originated and have become populous and successful they enter a period of stasis which is terminated by extinction. Other authors, although not denying the frequent occurrence of extinction, believe to have also evidence for a great deal of phyletic transformation.

b) Termination of a species in a single lineage through its transformation (by phyletic gradualism) into one descendant species. As stated above, the point of termination of the parental species is strictly arbitrary in such a case.

c) "Extinction" of a species when it subdivides by dichopatric speciation into two or more daughter species. The change that occurs in both of the daughter lineages is a slow transformational change. There is actually no genuine extinction of the parental species, only its gradual transformation into daughter species.

It is evident from this analysis that an unequivocal determination of the end point of a chronospecies can be made only when it becomes extinct in the traditional sense of the word (category (a)).

(5) "Operational" species definitions

Some recent authors have rejected the establishment of any species concept. Instead they propose to adopt an operational principle that would serve like a recipe telling the taxonomist in each case whether a given population is or is

not a different species. Among such operational principles the following are employed most widely.

(1) The difference principle. According to this principle species are "the smallest groups that are consistently and persistently distinct, and distinguishable by ordinary means" (Cronquist 1978 : 15). This means that every isolated subspecies would have to be called a species, while sibling species could not be recognized. Furthermore, since the word "groups" is not defined, males and females of sexually dimorphic species and any phena in polymorphic species, would have to be treated as different species. Such a procedure is, of course, nothing but the consistent application of the old typological species concept. It would not only lead to an enormous inflation in the number of recognized species, but these so-called species would be biologically completely meaningless. As we shall see, a somewhat similar approach is sometimes temporarily adopted by the working taxonomist when dealing with a group of species that have not yet been previously revised; but the subsequent testing with the biological species concept eventually permits the sorting of the tentatively recognized morphotypes into biological species.

(2) The recognition of all distinguishable geographical isolates as species. This principle was widely adopted in ornithology in the 1880 s and 90 s but was rejected when the polytypic species concept was adopted (Stresemann 1975).

(3) Recognizing species by cladistic principles. Hennig (1950), as explained above, recommended that any species be terminated when a sister or daughter species split off from it. This recommendation dealt with the delimitation of species in the time dimension. Rosen (1978, 1979) extended the principles of cladistics to the pattern of the geographic variation of species, and since he considered absence of reproductive isolation as a plesiomorphic character, the unerring logic of cladistics forbade him to use it as a character and this forced him to consider every geographic isolate that could be distinguished as a separate species. He then defined the species as "the smallest natural aggregation of individuals with a specifiable geographic integrity that can be defined by any current set of analytical techniques" (1979 : 277). Implicitly this is, of course, also a return to the pre-Darwinian concept of the typologically defined morphospecies.

Species delimited by such purely operational procedures are devoid of all biological significance. Their recognition may simplify the work of the museum curator, but they are of no use to a student of behavior, of ecosystems, or of biogeography. The weaknesses of operationism have been stressed sufficiently by Hull (1968) to make it unnecessary for me to add anything further.

FROM THE SPECIES DEFINITION TO THE DELIMITATION OF SPECIES TAXA

Both Ghiselin and Hull have rightly emphasized that one can not define individuals (or populations), one can only describe them. By contrast, a class

is characterized by its defining properties. The category species, being a class, therefore, can be defined. A species taxon, on the other hand, can only be described or delimited. To understand this difference is of the utmost importance for theory and practice of taxonomy at the species level. It makes it clear why it is so important to distinguish between taxon (individual) and category (class). One only needs to read the paper by Sokal and Crovello (1970) to see what utter confusion results from a neglect of making that distinction.

There can be little doubt that the concept of the biological species is what most modern biologists have in mind when they talk about species. They have had too much experience with all forms of polymorphism and with sibling species to find a typological or morphological species concept useful.

This poses a dilemma. How can one use the species definition when one's task is the delimitation of species taxa? The species definition is based on the nondimensional situation of the noninterbreeding of coexisting populations, where reproductive isolation can be observed directly. Species taxa, however, are multidimensional in area and in time. The question thus becomes : How can the "ideal" nondimensional species be expanded into a multidimensional species taxon?

As long as there is a continuity of populations, there is no problem. The gradual merging of such populations is *de facto* proof of interbreeding. A problem arises, however, whenever there are discontinuities either in nature or in our records. How can one combine populations into a species that are isolated geographically or in the time column (as encountered by the paleontologists)? In such cases conspecificity can be made probable only through inference; and such an inference can be made only by applying the yardstick of the biological species concept.

Inference. — In the case of populations separated by a gap, species status is determined by inference. In the case of geographical isolates as well as in phyletic series, one assumes conspecificity when no phenetic change exists. On the other hand, one assumes specific difference when the morphological difference is of the same order as is found among sympatric species of the same higher taxon. Here one must be aware of what is the premise and what is the conclusion. As Simpson has stated so beautifully (1961 : 68-69), two individuals are not identical twins because they are so similar, but they are so similar because they are identical twins. We do not "make" two populations a species because they are similar; rather, we conclude that they belong to the same species because they are so similar.

Morphological similarity is only a relative yardstick. It provides no certainty. We may find in the same genus (e.g. *Drosophila*) sibling species which by molecular analysis can be shown to be only rather distantly related, and morphologically distinct species that are very closely related. Not only may the rate of divergence in different isolates be different, but so may also be the rate of change in different characters. There are of course other clues concerning probable conspecificity, such as distribution, role in the ecosystem, life history attributes, etc. Much of that information is not available for fossil samples.

The great similarity of isolates to the parental species has often in the past been attributed to gene flow (Mayr 1963). This factor is indeed in part responsible for such uniformity. However, as Ehrlich and Raven (1969) have rightly pointed out, almost perfect similarity may be maintained in the virtual absence of gene flow. It is highly probable that such stasis is maintained by an internal cohesion of the genotype reinforced by stabilizing selection (Mayr 1970). This cohesion of the genotype affects in most cases not only the morphology but also the isolating mechanisms. It is one of the major problems of evolutionary biology to determine under what conditions these stability-maintaining mechanisms are broken down.

DIFFICULTIES IN THE APPLICATION OF THE BIOLOGICAL SPECIES CONCEPT

Species taxa consist of populations extending in space and time. The application of the biological species concept during the process of delimiting species taxa often encounters difficulties. I have discussed these in considerable detail in my *Animal Species and Evolution* (1963 : 21-29). Almost everything I said on that occasion is still valid. Very often a lack of pertinent information necessitates a provisional assignment of names to taxa. The morphological criteria generally used for a first approach can often be tested against behavioral, cytological, or molecular evidence.

It is sometimes claimed that different modes of speciation produce different kinds of species. On the whole this does not seem to be true. Species produced by dichopatric, peripatric, and sympatric (where it occurs) speciation are of the same kind. Changes in the chromosome number may cause difficulties, but polyploidy and other changes in chromosome number are rare in animals. They occur commonly in plants, and the status of some of the biotypes which differ in chromosome number is still controversial.

Hybridization, when resulting in fertile offspring, could give rise to reticulate evolution and thus be a special process of speciation. Again this seems to be far more common in plants than in animals. In animals, as White (1978) has shown, it almost invariably results in a switch to uniparental reproduction. In certain fishes and amphibians, stabilized hybrid species occur in the meiosis of which – or already during fertilization – the paternal genome is eliminated, and mating with a male of the paternal species is required to produce zygotes of the next generation (Dubois and Günther 1982). These stabilized hybrids behave in nature like good species. It is likely that similar cases will be found in other groups of organisms.

It is now quite evident that the evolutionary intermediacy of certain populations is the factor that poses the greatest difficulties in the delimitation of species taxa. All populations of a species that are geographically isolated follow their own evolutionary path. They may diverge more and more from the

parental population and become incipient new species. If all their characteristics would evolve at the same rate one might be able to accept a standard that would indicate completion of speciation. This, unfortunately, is not the case, and some populations may acquire reproductive isolation but only minimal morphological difference (resulting in sibling species) while others may acquire conspicuously different morphologies but no isolating mechanisms (Mayr 1963). Even closely related species usually differ in their enzymes, as revealed by electrophoresis, but in other cases electrophoresis has so far been unable to reveal such differences even though by other criteria the investigated populations are genuine species. Finally, different populations may acquire different niche utilizations but no differences in their isolating mechanisms. Such mosaic evolution forces the investigator to make subjective decisions concerning species status. Alas, evolution, being as capricious and opportunistic as she is, will inevitably produce situations that do not allow for a totally satisfactory resolution.

I have discussed such cases of evolutionary intermediacy in great detail in two previous publications (1963; 1969 : 181-197). Actually, neither sibling species, nor drastic polymorphism, nor occasional hybridization pose many practical problems when properly analyzed. What is controversial most frequently is the question whether certain geographical isolates should or should not be considered full species (allospecies), and in a mature taxonomy, as that of birds, this uncertainty causes the only major disagreement among different workers. A similar situation seems to prevail in freshwater fishes, where certain workers (e.g. Rosen 1979) have recently raised all subspecies to species level. Whether to call such isolates subspecies or species is in most cases quite irrelevant, because the ecologist and in most cases also the student of behavior, deals with the interaction of sympatric populations, and the potential status of an allopatric population is usually biologically rather uninteresting.

AGAMOSPECIES

Since the reproductive isolation of populations is the criterion of species status in the biological species definition, it is difficult to apply this concept to asexually reproducing clones. When there is no interbreeding, the term population is not appropriate, and this invalidates any definition for agamospecies which uses the word population. Uniparental reproduction is very widespread in the plant kingdom, but much less so among animals. I have discussed at an earlier occasion (1969 : 30, 46-47) what criteria one might use for the recognition of species in uniparentally reproducing organisms. What one generally does is to assemble clones on the basis of degree of similarity, but one can also use niche occupation as an additional criterion. There are often discontinuities between the niches of different sets of clones (see also Mayr 1963 : 27-29).

The biological species concept was developed for sexually reproducing higher organisms. Applying the term species to other kinds of organisms is

done by analogy. Some authors believe that such an analogy is inappropriate and favor instead a pluralism of species concepts. I discussed "kinds of species" at an earlier occasion (1963, Chapter 14) and came to the conclusion that there is a great deal of overlap among the various possible ways of distinguishing between kinds of species. In most cases recognizing such species consists of going back to an essentially morphological or typological species concept. Species are biological entities, and the recognition of this fact takes precedence over any specific needs of taxonomists.

THE SIGNIFICANCE OF SPECIES IN BIOLOGY

Modern biologists are almost unanimously agreed that there are real discontinuities in organic nature, which delimit natural entities that are designated as species. Therefore the species is one of the basic foundations of almost all biological disciplines. Each species has different biological characteristics, and the analysis and comparison of these differences is a prerequisite for all other research in ecology, behavioral biology, comparative morphology and physiology, molecular biology, and indeed all branches of biology. Whether he realizes it or not, every biologist works with species.

The diversity of organic life, consisting of species and groups of species (higher taxa), is the product of evolution. This necessitates the study of the origin and evolutionary history of every species and higher taxon. The study of species is thus shown to be one of the fundamental preoccupations of biology. And no such study will be constructive unless based on a sound species concept. This is the reason why a deep understanding of the nature of species is of such utmost importance.

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